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THE FAUNA OF WATER-FILLED TREE HOLES IN BOX FOREST IN SOUTH-EAST QUEENSLAND

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Abstract

Samples of detritus from a series of water-filled tree holes in box forest in south-east Queensland have been examined and the species encountered are discussed. Altogether nine "dendrolimnetobiontic" species are recorded: a chironomid, a ceratopogonid, two species of culicid, an helodid, three species of mite and a frog. All species spend their immature life in tree holes and, in addition, adult mites and, on one occasion, frogs were encountered. The trophic relations of the species concerned are discussed and are placed in context of work done elsewhere.

Introduction

Water-filled tree holes are a common component of moist forest ecosystems throughout the world. Everywhere that they have been studied these habitats have been shown to contain species of insects and other animals which in most instances occur nowhere else. These organisms have been designated "dendrolimnetobionts" by some authors (Rohnert, 1950; Kitching, 1971).

Water-filled tree holes occur in many Australian ecosystems from tropical forests to urban gardens but achieve semi-permanent status only in moist coastal forests. Although a variety of culicids and ceratopogonids have been recorded from these water bodies (Dyce and Murray, 1966, 1967; Hamlyn-Harris, 1933; Kettle and Elson, 1976; Lee and Reye, 1953; Marks, 1947; Reye, 1964) no systematic study of the whole community of macro-organisms has been carried out in Australia. Some such studies have been made elsewhere in the world and these are reviewed by Thienemann (1934), Kitching (1971) and Maguire (1971).

This paper presents a preliminary account of the results of such a survey together with some notes on the physico-chemical nature of the habitat. A monthly survey designed to shed light on the population dynamics of the animals concerned is in progress.

Study site and methods

Water-filled tree holes in the buttress roots of brush box (*Tristania conferta* R.Br.) and strangler fig (*Ficus* spp) were selected for study. An area of relatively undisturbed forest in the Lamington National Park (grid reference P14 on Northern Sheet; Queensland Department of Forestry, Edition 1, Lamington, 1: 25,000, 1975) was visited on a number of occasions and small samples of water and detritus removed from thirteen holes. A number of other sites were visited less regularly. Each of the thirteen regularly visited sites is lined with bark and has contained detritus and free-water throughout the period of observation (July, 1979 to August, 1980).

Water samples were removed using a plastic vial and detritus samples collected by hand or using a spoon. Samples were, later, washed through a series of sieves and the sludge remaining on the finest of these (355 μm) was washed into petri dishes and examined using a binocular microscope.

Insect larvae from the samples were sorted and reared to adulthood so that accurate identifications could be made. In addition, some observations on the behaviour of living larvae kept in petri dishes were made in order to determine the trophic relationships among members of the community.

In addition to these biological observations, measurements of the dimensions of the holes and their height from the ground were made as were records of the pH, conductivity and oxygen content of the water contained in them.

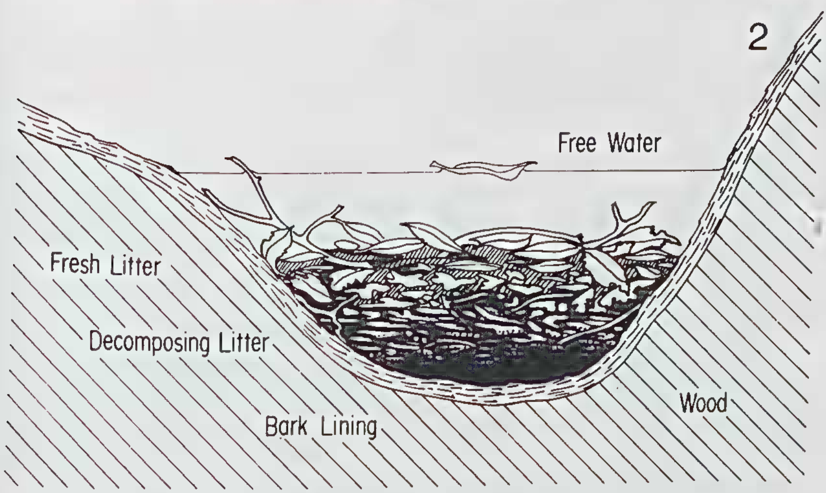
Results

The physical and chemical environment

Of the 20 holes sampled, 17 were from box trees and 3 from figs. The fauna in the samples from the two species of tree did not differ significantly.

The maximum diameters of the holes studied varied from 10-70 cm with a mean of 31.1 (SE = 3.59) and the minimum diameters had a range from 8-27 cm, with a mean of 15.3 (SE = 1.56). If we make the simplifying assumption that the surfaces of the holes were elliptical in shape, this gives us a range of surface areas from 78-1429 cm^2 about a mean of 422 cm^2 (SE = 99.24). The depths of the holes sampled ranged from 3-50 cm with a mean value of 16.3 cm (SE = 3.16) and the lips of the holes were from 0-150 cm above the nearest soil level (mean 34.3, SE = 8.72).

The chemical measurements were made on water samples from only nine holes and, therefore, their preliminary nature is stressed; nevertheless, they do provide an indication of the limnological conditions experienced by the fauna. The pH recorded spanned a range from 5.1-7.1 with a mean of 5.9 (SE = 0.23); the conductivity, a range of 143-288 $\mu s\ cm^{-1}$ at 25°C with a mean of 226.5 (SE = 75.5); and, the level of dissolved oxygen, a range of 10-55% saturation about a mean of 30.2 (SE = 5.24).



Figs 1, 2. Water-filled tree holes: (1) photograph of a water-filled tree hole in the root buttress of a box tree; (2) schematic cross-section through a water-filled tree hole showing layering of the detritus it contains.

Both the physical and chemical data point up the considerable variability in the nature of the tree hole habitat that has been remarked upon elsewhere (Kitching, 1969).

Figures 1 and 2 illustrate the tree hole habitat both photographically and schematically. Virtually all of the energy input to the tree hole system is through the entry of plant or animal detritus although strands of a filamentous algae were noted at one site. Some input of energy in run-off from the surface of the tree during rain is also likely. The eggs of the animals living in the holes represent a further, minor, energetic input.

The fauna

In all we found eight species of invertebrates and one vertebrate which can usefully be termed dendrolimnetobionts. These were two culicine mosquitoes, a chironomid midge, a ceratopogonid midge, an helodid beetle, three species of aquatic mite and a leptodactylid frog. Water-filled tree holes represent the larval medium for all of these nine with adults of the mites and, occasionally, the frog sharing the habitat. A variety of other insect larvae were encountered in the litter from damp holes (that is, those with no layer of free water) but these cannot be ascribed to a specialised aquatic fauna comparable with those studied elsewhere.

Of the nine species, four have been described previously, one is undescribed but represented by labelled specimens in a recognised collection, and four are in process of separate description, one of them representing a new genus (see below).

1. *Anatopynia pennipes* Freeman, 1961 (Diptera: Chironomidae: Tanypodinae)

Both larvae and pupae of this midge occurred in our samples. They were present in all 13 sites visited regularly with densities which ranged from 9.5 - 310 l^{-1}.

The species was described by Freeman (1961) from three adults collected by Bancroft at Burpengary, Queensland. The adult midges are highly distinctive having a broadly-banded wing pattern and "banded and thickly haired legs" among other characteristics. The larva is red in colour and characterised (in the tree-hole fauna) by its possession of prothoracic and terminal pseudopods and paired bunches of setae at its posterior end.

The general facies of the larva correspond closely with that illustrated by Bryce and Hobart (1972) as typical of the subfamily. Tanypodinae in general are predatory in their larval stages and, according to Bryce and Hobart, prey "on small invertebrates including other chironomid larvae". We exposed living larvae of *Culicoides angularis, Prionocyphon* and mosquitoes (see below for specific accounts) to living larvae of *A. pennipes* in petri dishes and observed them regularly. The chironomids frequently attached themselves by their anal pseudopods to helodid larvae and attacked the larvae with their mandibles. Attacks on mosquito larvae were noted, also, but no interaction except mutual aversion when in physical contact, was observed between chironomid and ceratopogonid. The relative abundances of the helodids, mosquitoes and the chironomids observed in our samples strongly suggest these are the principal predator-prey interactions in the tree-hole system. The occurrence of a tanypodine chironomid in these sites is somewhat at odds with records from elsewhere in the world where saprophagous orthocladines, notably species of *Metriocnemus,* have comprised the chironomid component (Kitching, 1972a; Snow, 1958).

2. *Culicoides angularis* Lee and Reye, 1953 (Diptera: Ceratopogonidae: Culicoidinae)

Again, both larvae and pupae of this species occur in water-filled tree holes. The species occurred in 12 of the 13 sites examined closely, with densities from 6.7-251 l^{-1}.

Lee and Reye (1953) described the species from Mittagong, N.S.W., from adults bred from larvae collected in a "rock pool". They also refer to other specimens from Mt. Glorious, Queensland and Cooranbong, N.S.W., all from water-filled tree holes. The Mt. Glorious locality is referred to again by Reye (1964) who describes the species there as "rare". The adult is distinguished by its large size and the pale spot in cell M_4 of the wing. The larva is figured by Kettle and Elson (1976) and has a characteristic vermiform shape with distinctive posterior filaments. Kettle and Elson (1976) record larvae of this species as being predatory and observed them feeding on free-living nematodes. Observations elsewhere in the world strongly suggest that they may prey on mosquito and other larvae under natural conditions.

This species is one of two ceratopogonines described from tree holes in Australia, the other being *C. mackerrasi* Lee and Reye; however, it is the only one recorded from moist, closed forest, the other having been found in holes in eucalypts and a species of *Acacia* (Dyce and Murray, 1966, 1967).

Tree-hole ceratopogonines recorded elsewhere have been species of *Dasyhelea* for the most part (Kitching, 1972b; Rohnert, 1950), although Kremer (1965) records several species of *Culicoides* from tree holes in the old world, principally Africa.

3. *Aedes (Finlaya) candidoscutellum* Marks, 1947 (Diptera: Culicidae)

This and the following species of mosquito have their larval and pupal stadia in water-filled tree holes. *Ae. candidoscutellum* was described by Marks (1947) from adults bred from larvae taken in tree holes in Queensland, New South Wales and New Guinea although the type specimens selected were from Binna Burra, Lamington National Park, a few kilometres from our study site.

The species occurred in 8 of 28 samples with densities ranging from 2.3-9.2 l^{-1}. The larvae are presumed to be grazers and/or suspension feeders, exploiting the smallest detrital particles and the micro-organisms associated with them.

4. *Aedes (Finlaya)* Marks, Species 22 (Diptera: Culicidae)

Dr E. M. Marks identified this material as belonging to an unnamed species known to her and designated "Marks: Species 22" in the University of Queensland collection housed at the Queensland Institute of Medical Research, Herston, Brisbane. The species is allied to *Aedes quasirubithorax* (Theobald). The frequency of occurrence of this species was much the same as the preceeding one but with densities ranging from 2.3-56.7 l^{-1}. This species too, presumably, is a grazer and suspension feeder as a larva.

5. *Prionocyphon* sp., ANIC Accession Designation "KIT1" (Coleoptera: Helodidae)

This species was identified by Dr J. F. Lawrence, CSIRO, as an undescribed species belonging to the genus *Prionocyphon.* In appearance it resembles closely tree-hole beetles of the same genus recorded in Europe (Benick, 1924; Kitching, 1971) and North America (Snow, 1958; Petersen, 1953). The larvae (and eggs presumably) occur in water-filled tree holes but the final instar larvae leave their aquatic milieu to pupate elsewhere. Benick (1924) says (in translation): "When the time for pupation comes the larvae . . . climb up to the drier part and pupate there. In nature they are found in the upper part of the hole space". He was referring to the European *Prionocyphon serricornis* but we have observed similar behaviour in the species we encountered. We found pupae in dry leaf litter associated with the water filled portions of some holes, and, subsequently, reared out adult beetles.

The larvae are saprophagous, grazing the detrital fragments. This species occurred in high densities in all sites examined with densities ranging from 50 - 1665 l^{-1}.

A separate description of the species is being prepared by Lawrence and Kitching and will be published in due course.

6. *Arrhenurus* sp. (Acarina: Arrhenuridae)

A species of free-swimming, red water mite identified as belonging to the cosmopolitan genus *Arrhenurus,* by Dr B. M. O'Connor (Cornell University), occurred in low numbers in a proportion of the tree holes sampled. This is the first record of the genus in such habitats.

The species occurred in 4 of the 13 holes examined regularly with densities ranging from 6.1 - 48 l^{-1}.

Species of *Arrhenurus* are predators recorded from other freshwater habitats preying on small organisms or parasitic upon larger ones (Williams, 1980). The relative size, abundance and free-swimming habit of this species suggests that early instar insect larvae may be the most likely prey in the tree holes we studied.

7. *Cheiroseius* sp. (Acarina: Ascidae)

The rarest of the species of mite encountered in our samples, in fact found only once, belong to an undescribed species of ascid ascribed by Dr O'Connor to the genus *Cheiroseius.* They are crawlers living, presumably, in the detritus layer where the most likely prey species, again based on considerations of size and relative abundance are of a third type of mite belonging to the family Hyadesiidae.

8. *Hyadesiid* sp. (Acarina: Hyadesiidae)

A species (or possibly two closely related species) belonging to an undescribed genus of the small family Hyadesiidae, was the commonest sort of mite found in our samples (occurring in 7 of 13 sites with densities ranging from 7 - 88 l^{-1}).

These mites occur in the detritus layer of the tree holes and, on the basis of information on other members of the family elsewhere, are considered to be saprophages exploiting the small particle component of the resource.

This genus will be described in dur course by O'Connor and Kitching.

9. *Lechriotus fletcheri* (Boulenger) (Amphibia: Anura: Leptodactylidae)

In our spring samples, which followed a period of heavy rain, large numbers of eggs and larvae of this species of frog were present. It may be inappropriate to consider this species truly dendrolimnetobiontic as both Moore (1961) and Watson and Martin (1973) record it from a variety of ephemeral habitats in rain forests in eastern Australia and New Guinea. However, we include it because, at one time at least, it was the dominant element of the fauna as indicated by our samples.

The tadpoles, which were identified by Mr Glen Ingram, Queensland Museum, are distinguished by having the "anus on the right; terminal mouth . . . and the fact that the posterior part of the body forms a right angle with the tail" (Moore, 1961). They have the bluntly rounded tail of a bottom feeder and are known to be cannibalistic, feeding on eggs and smaller tadpoles. Presumably they also prey on the insect larvae which co-occur with them in the water-filled tree holes. On a single occasion we also found an adult of this species in a tree hole.

No frogs are recorded from temperate tree holes but other species have been recorded from other plant-held waters (e.g. Picado, 1913; Laessle, 1961).

Discussion

The restricted nature of the tree-hole fauna shown up by our studies parallels the situation observed elsewhere in the world. This restricted diversity no doubt reflects the extreme physical and chemical circumstances which they present to their inhabitants. Not only does water level change in response to local factors but oxygen levels, in particular, are particularly low, possibly reflecting a high biological oxygen demand generated by the high level of micro-organismic activity in the decaying detritus. To cope with low oxygen tension special respiratory adaptations such as the anal gills of the helodid larvae and the siphons of the culicid larvae are present. The redness of the chironomid larvae, however, is due more to material sequestered from prey animals than to respiratory haemaglobin such as is present in some non-tanypodine chironomid larvae (Bryce and Hobart, 1972).

Our observations of nine species of animal from water-filled tree holes, although including several new records, does not, of course, represent the full range of tree-hole animals in Australia. A wide variety of mosquitoes has been recorded from water-filled tree holes and these are largely summarised by Dobrotworsky (1965). Several of these records are of generalist species in the sense that they also occur in other aquatic habitats. Of those restricted to tree holes most are of the subgenus *Finlaya* of *Aedes* or of the genus *Tripteroides,* one species of which (*atripes*) is widely distributed in Eastern Australia. Dr E. N. Marks (pers. comm.) suggests that the genus may favour very small cavities, below the size of those we examined. Among other dendrolimnetobionts of particular interest is the record of Watson and Dyce (1978) who found nymphs of the megapodagrionid damselfly, *Podopteryx selysi,* in tree holes in northern Queensland, paralleling records of Corbet (1962) and others from tropical south-east Asia.

The trophic relationships that we propose from our studies are summarised in Fig. 3 where firm relationships are indicated by solid lines and putative ones by broken lines. Basically, we recorded four species of primary saprophage (the helodid, culicids and hyadesiid) and five species of predator (chironomid, ceratopogonid, arrhenurid, ascid and leptodactylid). It seems likely that the saprophages partition the basic detritus resource probably on the basis of particle size with the culicids and the arrhenurid dealing with very fine particulate matter and the helodids feeding on more coarsely divided material. The predators seem, from what little information we have, to be catholic in their tastes.

The food web which can be imputed from these results is more complex than that recorded from similar situations elsewhere. Kitching (1971) recorded no predators from British tree holes and North American studies such as that of Snow (1958) record a single predator, mosquito larvae of

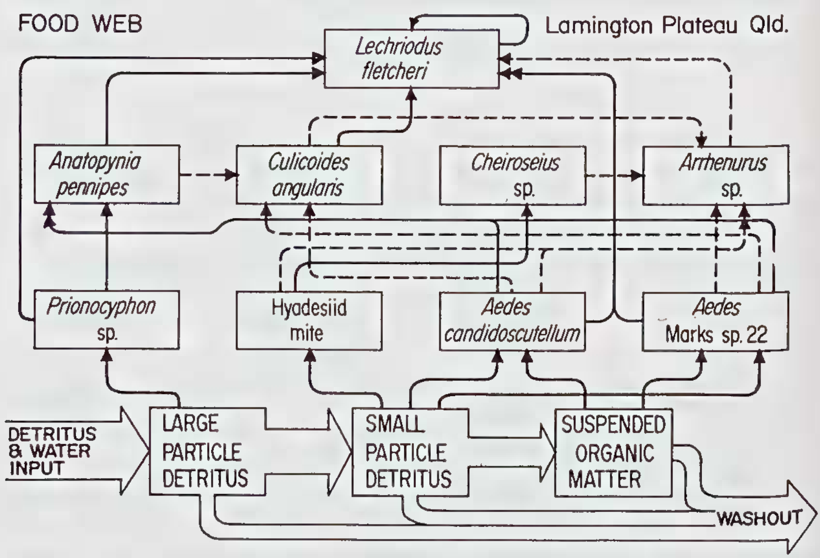


Fig. 3. Proposed food web for water-filled tree holes in south-east Queensland box forest based upon results of the present study. Solid lines indicate firm, and broken lines putative, relationships. In each case the head of the arrow indicates the consumer species.

the genus *Toxorhynchites.* Presumably the differences observed among these results reflects a response at the community level to the harshness of the environment and/or the quantity and quality of energy entering the system as detritus, acting through the conversion efficiencies of the species concerned. Further work is in progress on this aspect of the tree-hole community.

One of the principle complicating features of the Queensland food-web is the array of mites it contains. Mites are an endemic part of the tree-hole fauna in North America and, indeed, Fashing (1973, 1974) recorded both anoelid and acarid mites from such sites erecting a new sub-family, the Naiadacarinae, for his acarids. One other genus of the Hyadesiidae, *Algophagus,* is recorded from North American tree holes (B. M. O'Connor, pers. comm.). Mites occurring in scattered habitats such as water-filled tree holes must adopt parasitic or phoretic habits in order to move, as larvae, between sites. The host or transporting agents for other mites related to those encountered in this study, are known to be midges or mosquitoes to which the mites attach on emergence of the adult insect. In spite of extensive study, no mites have been recorded from European tree holes although sites in the south of that region await close examination.

Water-filled tree holes are just one of a wider class of plant-held waters usually referred to as phytotelmata. Other examples of such habitats are frequent in Australia but their faunas are largely unstudied. Among very few records is that of Dobrotworsky (1966) of *Aedes dobrotworskyi* Marks from water held in the leaf axils of swordgrass, *Gahnia* spp., and of Erickson (1968) of "the larvae of various mosquitoes and flies . . . and a very occasional tadpole" from *Nepenthes* pitchers and "slender, transparent larvae" from *Cephalotus* pitchers. Phytotelmata in leaf axils and stems of living plants and in fallen leaves and husks are common periodically in areas as different as rain forests and suburban gardens (especially where bromeliads are grown) and are deserving of further study.

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